A TWENTY-YEAR COMPARISON OF EPIGEIC SPIDER COMMUNITIES (ARANEAE) OF DANISH COASTAL HEATH HABITATS

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ABSTRACT. The same epigeic spider communities of North-west Jutland coastal heath habitats (Denmark, region Thy) initially surveyed by pitfall traps from 1977–79 were examined 20 years later (1997–98). The heath plots were open sandy areas growing into *Calluna* heath, and the more stable *Erica*, *Calluna/Empetrum*, *Molinia* vegetation types. They have changed vegetatively only a little in those 20 years from natural succession. Though the spider communities of all areas showed only minor changes from the passage of time, these were larger than the differences attributable to the different habitat types despite large differences in soil humidity and vegetation structure.

Keywords: Spiders, community composition changes, coastal heathland habitats, Denmark

The impact of habitat management on spider communities is usually analyzed by comparing variously treated or disturbed/undisturbed sites at the same point in time. Other studies have followed changes in the spider fauna associated with specific disturbances and the subsequent successional recovery by collecting over a series of years (heathland fires: Merrett 1976; forest fires: Huhta 1971, Schaefer 1980). Studies of long-term changes in the spider fauna of a particular site due to human modification of the biotope, pollution, vegetational succession, climatic change, or other causes are rare. Schikora (1994) found relatively minor changes over 22 years in the spider species of a bog in spite of prominent vegetation changes due to drainage. However, the dominant spiders had changed from photophilous to skotophilous species. Hänggi & Maurer (1982) compared the spider fauna of a Swiss raised bog after a 50-year interval, but the collecting methods were different. No known studies has analyzed the spider fauna of a specific locality by comparable methods over a long temporal scale.

Our aim in the present study is to compare the epigeic spider communities of four adjacent Danish coastal heathland habitats sampled by pitfall traps in the same locations with an interval of 20 years. We compare similarities in community composition both between habitats and between time periods. The vegetation of the area was only slightly affected by human activity in the intervening time. One site, which had been disturbed at the time of the first investigation, had been changed by vegetational succession during the 20 years.

METHODS

Site descriptions.—The study was carried out at Tørvekjær by Vester Vanned Sø, Thy, Denmark (57°1′30″N, 8°32′E). The area consisted of coastal heathland patches between an oligotrophic marsh to the south and sandy pastures and a coniferous plantation to the east and west. The plantation was established in the late 1950's and has provided increasingly more protection from the wind as it matured. The North Sea coast is *ca.* 3.5 km to the west.

Four points were sampled on a N-S transect perpendicular to low sandy ridges deposited by the prevailing westerly winds, which created alternating depressions and "hills" with varying vegetation. The differences in height between hills and depressions were never more than 0.5 m. However, the depressions could flood during winter, resulting in very divergent vegetational characteristics at the sites.

Traps 1–2 were situated on a hilltop, 3 m from the edge of a spruce plantation. In 1977–79 the traps were placed in a patch of bare

sand created by human disturbance. In 1997 the vegetation had recovered completely and grown into a typical dry heathland patch, dominated by *Calluna vulgaris* (L.) (coverage 50%), *Empetrum nigrum* L. (30%), and moss as groundcover.

Traps 3–4 were in a moist depression, 17 m from traps 1–2. The vegetation was dominated by *Erica tetralix* L. (90%) with moss covering the ground, and showed no recognizable changes between the two sampling periods.

Traps 5–6 were on a hilltop, 9 m from traps 3–4. The general character of the vegetation was dry dwarf-shrub heath. In 1977–79 it consisted of a mixture of *Calluna* and *Empetrum*; in 1997 *Empetrum* (70%) with moss groundcover was clearly dominant.

Traps 7–8 were in the next depression, 17 m from traps 5–6. In both sampling periods the vegetation was a nearly-pure dense stand of the low grass *Molinia caerulea* (L.) (>90%), indicating a very moist soil. Whereas the first three sites were dwarf-shrub heaths, this site was better characterized as a meadow.

Trapping.—Pitfall traps were used to monitor the active densities of ground-dwelling spiders at the selected sites. In 1977–79 glass jars (diameter 8 cm) were used, but in 1997 we used plastic beakers fitted into plastic flower pots (diameter 11 cm). A 3% formalin solution with ethylene glycol and detergent was used as a killing agent and preservative on both occasions. Trapping periods were 7 May 1977–23 March 1978, 13 May 1978–17 March 1979, and 11 May 1997–21 March 1998. The traps were emptied every 2–3 weeks during the warm seasons, and once a month or more infrequently during the winter periods.

Pitfall traps were placed in pairs at each site *ca.* 1–2 m apart. When trapping was repeated in 1997–98 the new traps were placed as close as possible to the same positions as was used earlier, all probably less than 2 m away.

The spider material is deposited in the collection of Zoological Museum, Copenhagen.

Weather.—We obtained weather information from the Danish Meteorological Institute. For 1977–79 data are from station Silstrup, for 1997–98 from Hørsted. Both are *ca.* 15 km from the study area. We used the monthly averages of temperature, sunny hours, and rainfall (Fig. 1).
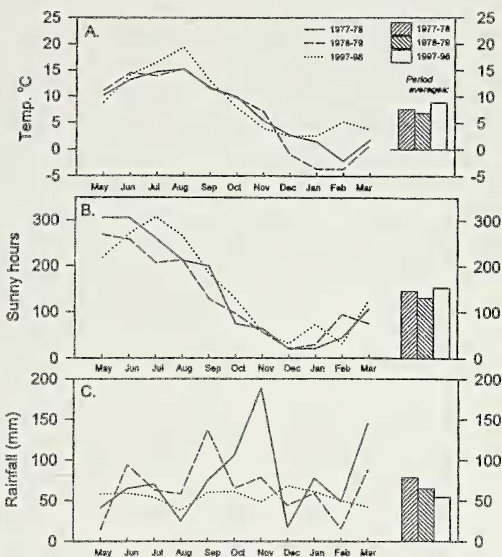

Figure 1.—Weather conditions during the three study periods, all plotted as monthly averages. A: Temperature (°C), B: Hours of sunshine, C: Rainfall (mm).

Overall 1997–98 was somewhat sunnier and warmer and with less precipitation than 1977–79. The average differences between the three trapping periods are quite small, and the conditions of 1997–98 do not deviate more from either of the early periods than from each other (Fig. 1).

Data analysis.—Comparison of the epigeic spider communities was made by Principal Component Analysis (PCA) using the CANOCO program (ter Braak 1987; cf. Jongman et al. 1987). We compared the summed catches for each site and catching period and applied the PCA to log-transformed abundances of each species. All species were included in the analyses (and thus in determining the relative distribution of the trap sites (Fig. 2)), but only the most dominant species (> 2% at one site and period) are presented in the species plot (Fig. 3). We also illustrate the species that disappeared or appeared between 1977–79 and 1997–98, as well as less dominant species (though > 0.4%) which showed substantial changes in relative abundance (Fig. 4). Additionally, we compared the dominance structure and species composition of the habitats (Fig. 5), and analyzed the species changes between the two periods. Two similarity indices for pairwise comparisons (Southwood 1966) were calculated: the Sørensen Quotient of
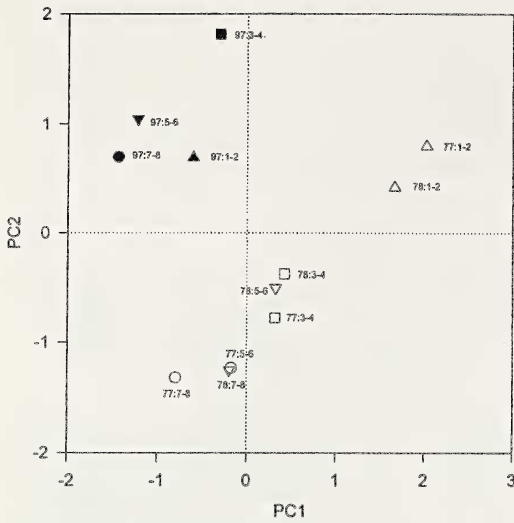
Figure 2.—Principal Component Analysis (site plot) of summed catches from each of four trap sites for three trapping periods (1977–78, 1978–79 and 1997–98). Starting year and trap-numbers indicated next to each point. Traps 1–2: Bare sand (1977, 1978) or *Calluna* (1997); Traps 3–4: *Erica*; Traps 5–6: *Empetrum/Calluna*; Traps 7–8: *Molinia*.
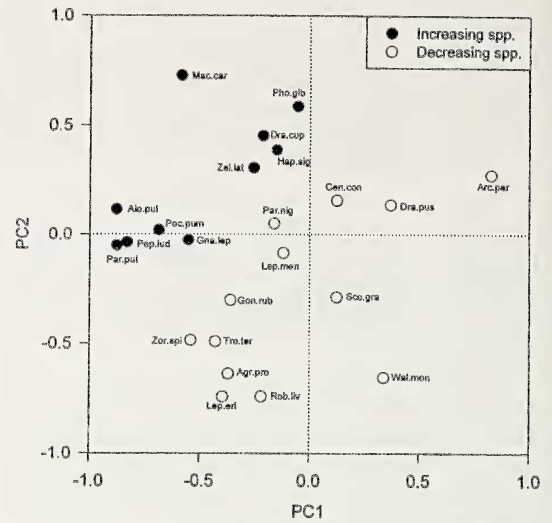

Figure 3.—Principal Component Analysis (species plot, same analysis as Figure 2) of summed catches from each of four trap sites for three trapping periods (1977–78, 1978–79 and 1997–98), illustrating dominant species (>2%). Abbreviations of species names: see Appendix 1.

similarity, $QS = 2j/(a + b)$, where a and b are the number of species in the two samples, and j is the number of species common to both samples; and the Percentage of similarity, $\%S = \Sigma_i \min (p_{ia}, p_{ib})$, which sums the lowest values for the proportional abundances (p) of each species (i) in the two samples (a, b).

RESULTS

Faunistic characteristics.—A total of 6368 specimens belonging to 113 species was collected, of which 23 species had a relative dominance of >2% in at least one site and year. The number of individuals and species at each site increased for 1997–98 compared to the earlier periods (Table 1). It can therefore

be concluded that there has been no decline in the richness of the spider fauna over the 20 years.

The number of species in common between the trapping periods was extremely stable (Table 2). It is remarkable that the number of species disappearing between 1977–78 and 1978–79 was the same as between 1977–78 and 1997–98. This may indicate that "disappearance" does not necessarily mean extinction but rather reflects chance of capture. Given the low number of traps in each habitat, this effect is not surprising. More new species seem to have accumulated over the 20 year period than between 1977–78 and 1978–79, but this may also be due to the higher number of individuals caught in 1997–98.

Table 1.—The number of individuals and species of spiders collected by two traps at each of four trapping stations during the three trapping periods.

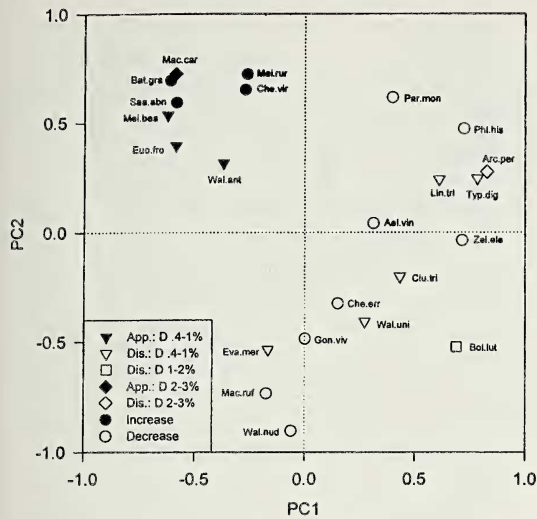|	1977–78		1978–79		1997–98	
	Ind.	Species	Ind.	Species	Ind.	Species
Traps 1–2	317	46	429	46	465	56
Traps 3–4	513	47	536	41	671	47
Traps 5–6	583	54	487	38	532	50
Traps 7–8	584	43	544	41	707	54
Total	1997	80	1996	71	2375	87

Figure 4.—Principal Component Analysis (species plot, same analysis as Fig. 2) of summed catches from each of four trap sites for three trapping periods (1977–78, 1978–79 and 1997–98), illustrating species appearing (App.) or disappearing (Dis.) between 1977–79 and 1997–98 (maximal dominance value (D) in year of presence indicated), and non-dominants showing substantial changes (increase/decrease) between these periods. Abbreviations of species names: see Appendix 1.

Principal component analysis.—Analysis of spider species abundances in each of the traps during every trapping period resulted in a plot of sites × years (Fig. 2) and corresponding plots of species distributions (Fig. 3, 4). The sites clustered in three groups (Fig. 2). One group consisted of traps 1–2 from 1977-78 and 1978-79; a second group was formed by all other sites for the same two periods, and the third group included the four sites from 1997-98. Thus, except for traps 1–2 in the early periods, the habitats do not cluster together while the catching periods do. This means that the temporal changes in the fauna

are more prominent than the differences between the habitats. Axis 1 (PC1) mainly reflects the changes resulting from vegetational succession at traps 1–2, while axis 2 (PC2) reflects the faunistic changes taking place at the remaining trapping sites over 20 years, which cannot be easily related to specific habitat changes. There seem to be no further relationships between the two PC-axes and characteristics of the habitats. The change of the spider community at traps 1–2 was expected because this site was a disturbed patch of bare sand, which succession eventually turned into a plant community similar to that of site 5–6. We repeated this analysis for spring/summer (May-September) and autumn/winter (October-March) catches separately. Both data sets gave the same pattern as for the full periods.

The dominant species were concentrated in the central part of the PC-plot (Fig. 3), reflecting a high similarity in species composition between the habitats within a period. This plot and the following (Fig. 4) show the differences in species composition responsible for the pattern in Fig. 2, and the axes should be interpreted similarly. Species in the upper left are those that increased in abundance after 20 years, while those to the right and in the lower part decreased. Species that either appeared or disappeared during the 20 years or had a relative abundance of < 2% showed a clear separation of increasing/appearing vs. decreasing/disappearing (Fig. 4).

Both types of similarity indices between years produced values between 70–80% (Table 2). The two early periods were not more similar than early versus late periods.

Dominance structure.—The same few species were the dominants in all four habitats (Fig. 5), with *Gnahosa leporina* (20) and *Centromerita concinna* (3) being at positions 1–3

Table 2.—Comparison of spider population characteristics between trapping periods (catches from different habitats summed for each year).

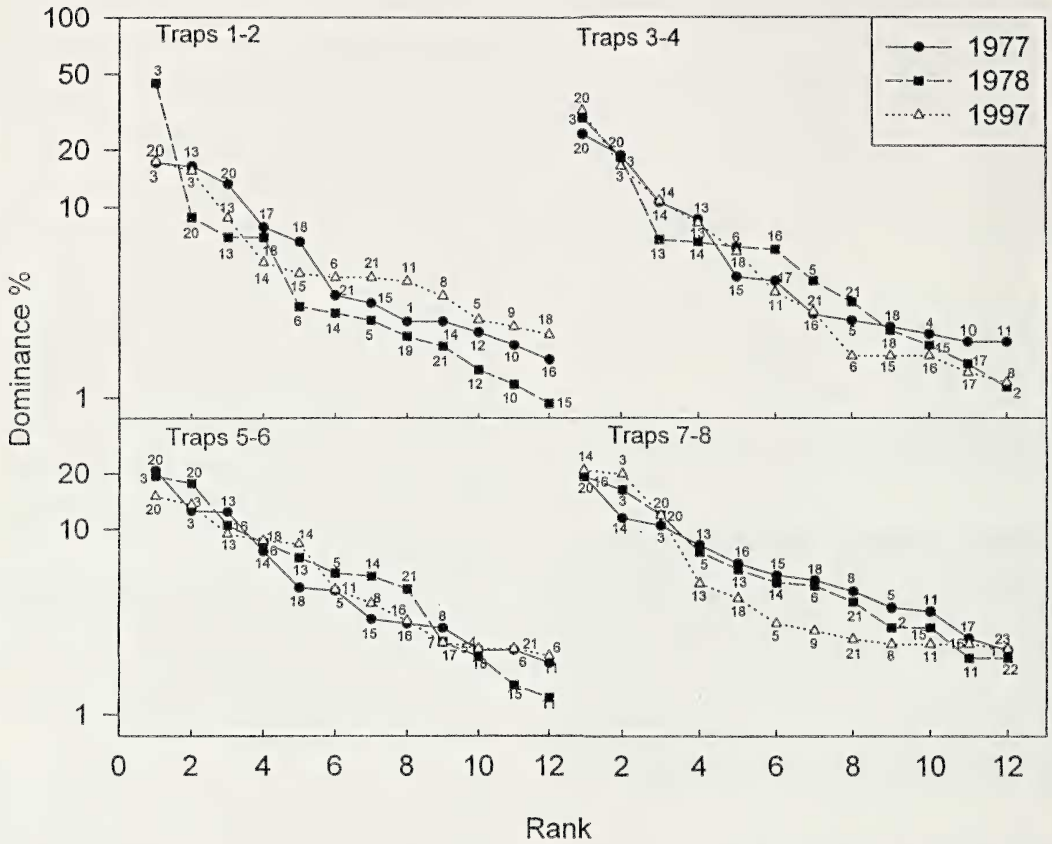|	77–78 vs. 78–79	77–78 vs. 97–98	78–79 vs. 97–98
Number species both periods	57	58	59
Number species disappearing	23	22	12
Number species appearing	14	27	28
Sørensen's quotient of similarity	75.5	70.3	79.7
Percent similarity	69.0	79.3	69.5

Figure 5.—Dominance curves for spider communities of four heathland trap-sites in three trapping periods (12 most abundant species only). Numbers indicate species identity (cf. Appendix 1).

in all habitats and years (Fig. 5). Only in the *Molinia* habitat they were surpassed by *Pardosa pullata* (14) and *Agroeca proxima* (16). *Pardosa nigriceps* (13) was codominant at the two "hilly" sites, while *P. pullata* had its highest dominance in the moist depressions. When comparing the four sites over the 20 years there are no indications of systematic changes in the dominance structure. Five species occurred with > 2% dominance in all years at all sites: *C. concinna, P. nigriceps, P. pullata, G. leporina,* and *Haplodrassus cupreus.*

Species appearances and disappearances.—At trap sites 1–2, several species preferring bare sandy areas were caught during 1977–79 but disappeared later when the vegetation closed. That was true for *Arctosa perita,* while *Pardosa monticola, Aelurillus v-insignitus* and *Zelotes electus* decreased in abundance. Some vegetation-dwelling species,

like *Linyphia triangularis* and *Philodromus histrio,* seemingly decreased. It is possible, however, that this is an artifact because they are found only on the soil surface if there is no vegetation.

Macrargus rufus declined at some sites while *M. carpenteri* appeared in considerable numbers in 1997–98. We are unable to relate this shift to the small habitat or environmental changes between the sampling periods. Increasing species (cf. Figs. 3, 4) include species that in Denmark are associated mainly with (dry) heathlands (*P. ludicrum, Z. latreillei, D. cupreus*), while others are hygrophilous (*M. beata*) or even moist heathland specialists (*G. leporina*).

Thus, it is impossible to determine a direction of change with respect to the ecological characteristics associated with species whose abundances changed.

DISCUSSION

Structural characteristics of the vegetation are generally thought to be the most important factor for habitat selection of spiders and thus for determining the composition of the spider fauna (Duffey 1962, 1966, 1968; Curtis & Bignal 1980; Robinson 1981). We therefore expected spider communities in different habitats to show large differences relative to the temporal changes, especially at the two sites where no vegetational changes had occurred. We observed the opposite in spite of great differences in vegetational physiognomy between some of the sites. The *Molinia* meadow and the *Calluna/Empetrum* heathland sites were very different both in vegetation structure and soil moisture; the *Erica* and *Molinia* sites were similar in soil moisture but different in vegetation structure, and the *Erica* and the *Calluna/Empetrum* sites were somewhat similar in vegetational structure (all dwarf shrubs) but different in soil moisture. Yet, all were quite similar in their spider fauna. We found relatively large differences between bare and vegetated habitats, probably because bare sandy areas are without vegetational structure and also microclimatically extreme. Several xerophilic spider species are specialists of this habitat type.

Temporal changes in the spider community composition were greater than differences between habitats. This was not due to any dramatic changes over the years in the composition of the spider communities, however, because even these changes were quite small. This is not only evident from the high similarities, but also from a consideration of the specific changes. For example, the most abundant species that disappeared had a dominance score of only 2.2% at the site of highest abundance (*Arctosa perita* at traps 1–2). The appearing species that became most abundant reached a dominance score of 2.4% (*Macrargus carpenteri* at traps 5–6). Among the dominants the greatest difference in dominance score between 1977–79 and 1997–98 (all sites combined) was <5%. Thus, viewed over the 20 years, the composition of the spider fauna has been very stable. On a still longer time scale these communities will certainly not be maintained; most likely the area will be invaded by shrubs (a process already started) and eventually trees, and thus the vegetation type will change completely, unless maintained by management. This development is accelerated by the planting of the forest that surrounds the heathland area, creating a much milder microclimate than before and providing invasive tree species.

The reasons for the temporal changes should be considered. For trap-sites 1–2, vegetational succession following a disturbance is the obvious cause. For the remaining sites the question is more difficult. We could see no pattern in the ecological preferences of species that decreased/disappeared or appeared/increased. The weather in 1997–97 was slightly warmer and dryer than before, but it is difficult to relate the specific faunistic changes to this fact, since the differences between the two early periods are as large as between early and late periods.

LITERATURE CITED

Curtis, D.J. & E.M. Bignal. 1980. Variations in peat bog spider communities related to environmental heterogeneity. Pp. 81–86, *In* Proc. 8th Internat. Congr. Arachnol., Vienna.

Duffey, E. 1966. Spider ecology and habitat structure. Senckenbergiana Biol., 47:45–49.

Duffey, E. 1968. An ecological analysis of the spider fauna of sand dunes. J. Anim. Ecol., 37:641–674.

Duffey, E. 1962. A population study of spiders in limestone grassland: the field-layer fauna. Oikos, 13:15–34.

Huhta, V. 1971. Succession in the spider communities of the forest floor after clear-cutting and prescribed burning. Ann. Zool. Fennica, 8:483–542.

Jongman, R.H.G., C.F.J. ter Braak & O.F.R. van Tongeren. 1987. Data Analysis in Community and Landscape Ecology. Pudoc, Wageningen. 299 pp.

Merrett, P. 1976. Changes in the ground-living spider fauna after heathland fires in Dorset. Bull. British Arachnol. Soc., 3:214–221.

Robinson, J.V. 1981. The effect of architectural variation in habitat on a spider community: an experimental field study. Ecology, 62:73–80.

Schaefer, M. 1980. Sukzession von Arthropoden in verbrannten Kiefernforsten. II. Spinnen (Araneida) und Weberknechte (Opilionida). Forstwiss. Centralbl., 99:341–356.

Schikora, H.-B. 1994. Changes in the terrestrial spider fauna (Arachnida: Araneae) of a North German raised bog disturbed by human influence. 1964–1965 and 1986–1987: a comparison. Mem. Entomol. Soc. Canada, 169:61–71.

Southwood, T.R.E. 1966. Ecological Methods. Me-
    thuen & Co. Ltd., London.
ter Braak, C.J.F. 1987. CANOCO (version 2.1).
    Agricultural Mathematics Group, Wageningen.
    95 pp.

APPENDIX 1

Nomenclature, name abbreviations and number
codes for species mentioned in text and figures.

Ael.vin	*Aelurillus v-insignitus* (Clerck)
Arc.per	*Arctosa perita* (Latr.)
Agr.pro	*Agroeca proxima* (O.P.-C.) (16)
Alo.pul	*Alopecosa pulverulenta* (Clerck)
Bat.gra	*Bathyphantes gracilis* (Bl.)
Bol.lut	*Bolyphantes luteolus* (Bl.)
Cen.con	*Centromerita concinna* (Thor.) (3)
Che.err	*Cheiracanthium erraticum* (Walck.)
Che.vir	*Cheiracanthium virescens* (Sund.)
Clu.tri	*Clubiona trivialis* C.L.K.
Dra.cup	*Drassodes cupreus* (Bl.) (18)
Dra.pus	*Drasyllus pusillus* (C.L.K.) (19)
Euo.fro	*Euophrys frontalis* (Walck.)
Eva.mer	*Evansia merens* O.P.-C.
Gna.lep	*Gnaphosa leporina* (L.K.) (20)
Gon.rub	*Gonatium rubens* (Bl.) (4)
Gon.viv	*Gongylidiellum vivum* (O.P.-C.)
Hap.sig	*Haplodrassus signifer* (C.L.K.) (21)
Lep.eri	*Lepthyphantes ericaeus* (Bl.) (5)
Lep.men	*Lepthyphantes mengei* Kulcz. (6)
Lin.tri	*Linyphia triangularis* (Clerck)
Mac.car	*Macrargus carpenteri* (O.P.-C.) (7)
Mac.ruf	*Macrargus rufus* (Wider)
Mei.bea	*Meioneta beata* (O.P.-C.)
Mei.rur	*Meioneta rurestris* (C.L.K.)
Par.mon	*Pardosa monticola* (Clerck)
Par.nig	*Pardosa nigriceps* (Thor.) (13)
Par.pul	*Pardosa pullata* (Clerck) (14)
Pep.lud	*Peponecranium ludicrum* (O.P.-C.) (8)
Phi.his	*Philodromus histrio* (Latr.)
Pho.gib	*Pholcomma gibbum* (Westr.) (1)
Rob.liv	*Robertus lividus* (Bl.) (2)
Saa.abn	*Saaristoa abnormis* (Bl.)
Sco.gra	*Scotina gracilipes* (Bl.) (17)
Tro.ter	*Trochosa terricola* Thor. (15)
Typ.dig	*Typhocrestus digitatus* (O.P.-C.)
Wal.ant	*Walckenaeria antica* (Wider)
Wal.mon	*Walckenaeria monoceros* (Wider) (10)
Wal.nud	*Walckenaeria nudipalpis* (Westr.)
Wal.uni	*Walckenaeria unicornis* O.P.-C.
Zel.ele	*Zelotes electus* (C.L.K.)
Zel.lat	*Zelotes latreillei* (Simon) (22)
Zor.spi	*Zora spinimana* (Sund.) (23)